FOOD-NICHE PARTITIONING AMONG SYMPATRIC KINGFISHERS IN BHITARKANIKA MANGROVES, ODISHA

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The study, conducted from January to May, 2011, attempted to understand the potential mechanisms that may play a role in food-niche differentiation among four sympatric kingfishers, i.e. Small Blue, Collared, Black-capped, and Brown-winged kingfishers in Bhitarkanika mangroves. For foraging behaviour, an individual was followed till it captured a prey and relevant foraging variables were recorded. A total of 53 independent prey captures were recorded for the four species of kingfishers. Perch height and foraging distance differed significantly among the four kingfisher species. All the prey characteristics, i.e., prey type, prey size, and foraging substrate showed significant variations among the species. This study revealed that each of the four kingfisher species in Bhitarkanika mangroves occupy foraging niches corresponding to their respective body size. The foraging behaviour of the smallest species, i.e., Small Blue Kingfisher, and the largest, i.e., Brown-winged Kingfisher, is similar. The foraging behaviour of the Collared and Black-capped Kingfisher is similar, but they differ in terms of prey size taken, corresponding to their respective body sizes.

Key words: Kingfisher, foraging, mangroves, prey

INTRODUCTION

Kingfishers are a cosmopolitan group of stockily built birds with characteristic colourful plumage, short neck, and dagger-like bills (Knowles and Nitchen 1995). This large and widespread family consists of 93 species worldwide, with 12 residents and one vagrant species in India (Rasmussen and Anderton 2005). They are known to inhabit a wide range of habitats, e.g., rain forests, deciduous woodlands, savannahs, arid areas, mangrove swamps, freshwater swamps, lakes, sea shores, river valleys, and estuaries. Their food varies from small fish and water crustaceans to small vertebrates, insects, and arachnids. Kingfishers are diurnal, highly mobile, wide ranging and are relatively easy to observe. Moreover, several species of kingfishers are known to coexist in a given space and hence they are a good group to study food-niche partitioning.

Sympatric species with similar resource requirements need to partition available niche space in order to coexist. The search for these mechanisms underlying such species' coexistence is a central issue of community ecology (Begon *et al.* 1990). To understand these mechanisms, it is vital to know about the food requirements, foraging habitat preferences, and how the resources are shared between these sympatric species. Reduction of food-niche overlap may occur through food partitioning by type or by size of prey, or through segregation in foraging areas (Garcia *et al.* 2005). Our study attempted to understand the pattern of food-niche differentiation among four sympatric kingfishers, i.e., Small Blue *Alcedo atthis*, Collared *Todiramphus chloris*, Black-capped *Halcyon pileata*, and Brown-winged *Pelargopsis amauroptera* Kingfishers in Bhitarkanika mangroves. Previous studies (Ashmole 1968; Costa *et al.* 2008; Kasahara and Katoh 2008; Padilla *et al.* 2007) have shown that prey size is determined by the body size of sympatric species. So sympatric kingfishers of different body sizes in Bhitarkanika were expected to show dissimilar prey size. Apart from this, there might be other inter-specific variations in foraging behaviour reflecting the influence of body size, e.g., perch height, foraging distance, and depth of water in the foraging site.

STUDY AREA

Bhitarkanika National Park (20° 30' – 20° 48' N; 86° 45' – 87° 03' E) is located in the deltaic region of Brahmani and Baitarani rivers in the Kendrapara district of Odisha. It presents a salt tolerant, complex and dynamic ecosystem that occurs in tropical and subtropical inter-tidal regions. The intensive study area consists of four forest blocks, namely Bhitarkanika, Dangamal, Mahinsmada and Ragadapatia blocks with an area of *c.* 40 sq. km. The main river flowing through the area is Bhitarkanika. Numerous creeks of different sizes are located all along the river, which are mainly fed by tidal water, so they are dynamic in nature; some of the smaller creeks completely dry out during low tide. The vegetation along the creeks mainly consists of tree species, such as

Table 1: Variables recorded on foraging behaviour of Kingfisher species in Bhitarkanika N.P. (Jan–May, 2011)

S. no	Variables	Remarks
1	Kingfisher species	Small Blue, Collared, Black-capped, or Brown-winged Kingfisher
2	Type of perch	Categorised as i) plant, ii) dry log, iii) bank, iii) artificial pole
3	Perch height	Height at which the bird perched while feeding – estimated visually in metres
4	Foraging distance	Distance travelled to catch the prey – estimated visually in metres
5	Water depth	Measured in metre at the visually determined point after the foraging individual flew away
6	Foraging substrate	The material from which food was taken; categorised as i) water, ii) vegetation, iii) tree hole, iv) mud bank, v) air
7	Size of prey	Estimated by comparing it with the bird's bill (as % of bill length) and categorised as i) small (less than the bill length of the smallest species Small Blue Kingfisher, i.e., <4 cm), ii) medium (all between small and big category, i.e., 4-8 cm), iii) big (greater than the bill length of the largest species Brown-winged Kingfisher, i.e., >8 cm)
8	Type of prey	Categorised as i) fish, ii) crabs, iii) insects, iv) mudskipper
9	Vegetation cover	% foliage cover imagining a circular plot of 5 m radius around the bird at 5 m distance from the perch site of the bird

Heritiera fomes, *Sonneratia apetala*, *Avicennia officinalis* and *Excoecaria agallocha*. Among shrubs, *Brownlowia tersa* is the most abundant species along the creeks.

METHODS

Foraging behaviour

The study was conducted from January–May 2011. Observation protocols were standardised after making *ad libitum* observations in the field (Altmann 1974). Efforts were made to record foraging observations from all types of habitats. The creeks were surveyed by country boats and individuals of the target species were actively searched. Observations were done opportunistically and once an individual of the target species was located, it was followed till it captured a prey and relevant foraging variables were recorded (Table 1). To reduce the problem of pseudo-replication, no further data was collected on the same species within 500 m of that site after recording an observation. All the data were recorded verbally into a dictaphone.

Analyses

Inter-specific variations in microhabitat variables, such as perch height, foraging distance and vegetation cover were tested using one-way ANOVA (Zar 1999). Prior to analyses, vegetation cover and foraging distance values were square root-arcsine and log (x+1)-transformed respectively.

To test for differences in prey characteristics, prey type, prey size, and foraging substrates across species, non-parametric Fisher's Exact Test of probability (Siegel and Castellan 1988) was used as the sample sizes were low. Correspondence analysis was conducted to visualise the kingfisher species on a multi-dimensional space in relation to the prey characteristics.

RESULTS

A total of 53 independent prey captures were recorded for the four species of kingfishers during the study period (Table 2).

Microhabitat variables

Perch height differed significantly (ANOVA: $F_{3, 49}$= 5.153, P = 0.004) among the four species of kingfishers, with the mean perch height of Small Blue Kingfisher *Alcedo atthis* being the lowest and that of Brown-winged Kingfisher being the highest (Fig. 1a). The foraging distance, i.e., the distance covered by a species to capture a prey also differed significantly (ANOVA: $F_{3, 49}$ = 7.520, P = 0.000). Difference in water depths used for capturing prey was tested only for Small Blue and Brown-winged Kingfishers, since the other two species did not pick prey from water. It did not vary significantly between the two species (t-test, t=0.539, df=25, P = 0.594). The vegetation cover used by the four species did not show any significant difference (ANOVA: $F_{3, 49}$= 0.926, P = 0.435). Post-hoc tests revealed that the distance covered by Small Blue and Collared Kingfisher for foraging is less than Black-capped and Brown-winged Kingfisher (Fig. 1b).

All the variables were not used to visualise a multivariate niche, as two species had no observation for one of the variables (water depth) and the four species did not differ significantly in the vegetation cover they used. In order to visualise the overall foraging niche-partitioning of the four species along the two variables (perch height and foraging distance) which differed significantly across the four species, individual observations were plotted along these two axes (Fig. 2). Based on the biplot, it is evident that Small Blue and Collared Kingfisher occupy relatively smaller foraging niches than Black-capped and Brown-winged Kingfishers (Fig. 2).

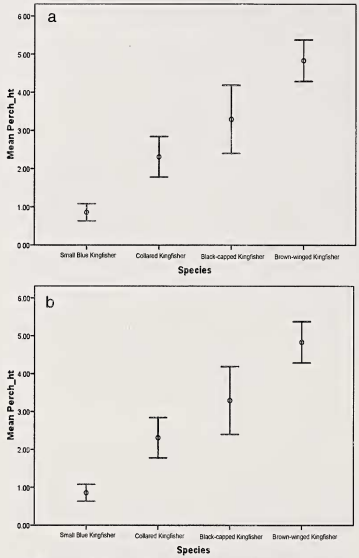

Fig. 1: (a) Perch height (mean ± 1SE), (b) foraging distance (mean ±1 SE) used for foraging by the four species of kingfishers in Bhitarkanika mangroves (Jan–May, 2011)

Among the prey characteristics, prey type differed significantly among the four species of kingfishers (Fisher's exact test, $P < 0.05$). Small Blue and Brown-winged

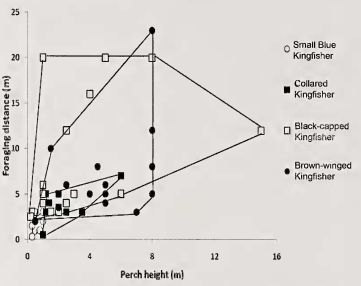

Fig. 2: Foraging-niche of the four species of kingfishers in terms of perch height (m) and foraging distance (m) in Bhitarkanika mangroves (Jan–May, 2011)

Kingfisher seemed to prefer fish more than other prey types (Fig. 3a). The Brown-winged Kingfisher feeds on mudskippers and crabs. The diet of Collared and Black-capped Kingfisher mainly consists of insects and crabs, respectively. Size of prey captured by each species also differed significantly (Fisher's exact test, $p=0.005$). Small Blue Kingfisher was observed to forage on small and medium prey, and a few large prey (Fig. 3b). Collared and Black-capped Kingfisher captured smaller prey than Small Blue and Brown-winged Kingfishers. Brown-winged Kingfisher foraged more on large prey than the rest of the three kingfisher species. The use of different foraging substrates among the four species of kingfishers also differed significantly (Fisher's exact test, $P<0.05$). Small Blue Kingfisher was seen foraging entirely in water (Fig. 3c). Brown-winged Kingfisher also preferred water as foraging substrate. In contrast, Collared Kingfisher mostly foraged in mud banks, vegetation, and tree holes to some extent.

Table 2: Summary of microhabitat variables affecting the foraging behaviour of each species of kingfishers in Bhitarkanika mangroves (Jan–May, 2011)

Species	Microhabitat variables				N ind
	Perch height	Vegetation cover	Foraging distance	Water depth	
Small Blue	0.86 ±0.6	0.53 ±0.2	1.98 ±1.1	0.41±0.4	9
Collared	2.31 ±1.5	0.54 ±0.2	3.78 ±1.8	0	9
Black-capped	3.29 ±3.6	0.52 ±0.2	8.44 ±6.6	0.06 ±0.2	17
Brown-winged	4.83 ±2.3	0.42 ±0.2	7.53 ±5.4	0.87 ±1.0	18
ANOVA, P	0.004	0.435	0.000	-	53
F	5.153	0.926	7.520	-	
Df	3, 49	3,49	3,49	-	

N ind - total no of total independent foraging observations

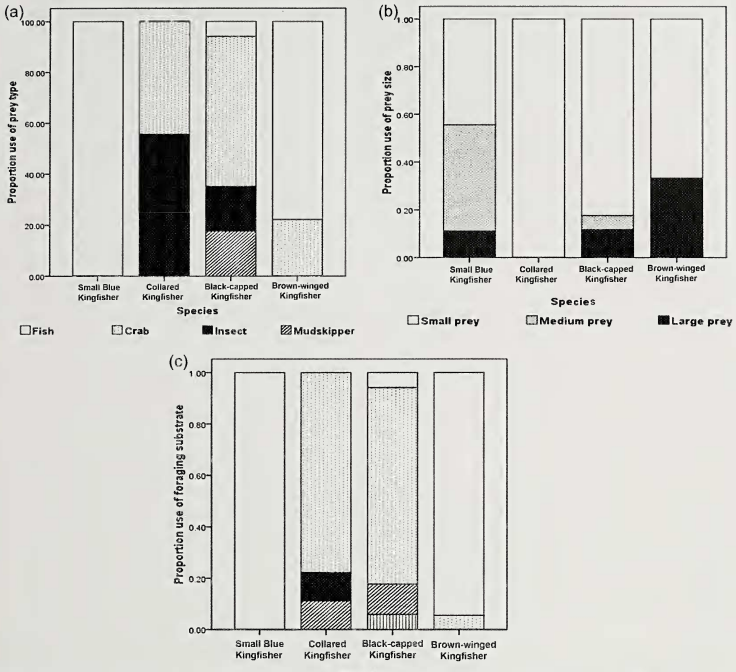

Fig. 3. Proportional use of (a) prey type (b) prey size and (c) foraging substrate by the four species of kingfishers in Bhitarkanika N.P., i.e., Small Blue Kingfisher (n=9), Collared Kingfisher (n=9), Black-capped Kingfisher (n=17), Brown-winged Kingfisher (n=18) (Jan–May, 2011)

Black-capped Kingfisher used four types of foraging substrates, most frequently mud banks, followed by air, water, and vegetation (Fig. 3c).

Correspondence analysis of prey characteristics resulted in one dimension (Fig. 4), which explained 91.9% variation in the data (Table 3). The axis reflected change in prey type from fishes to insects to crabs and mudskippers as we move from the negative to the positive end. Similarly, the axis represents a gradient in prey size, with higher scores indicating intake of smaller prey. While the use of water as a foraging substrate is indicated by lower scores, increasing score is associated with greater use of mud bank. Therefore, the species on the negative side of the axis, i.e., Small Blue and Brown-winged Kingfisher are associated with capturing fish from water (Fig. 4), whereas species placed in the positive part, i.e., Collared and Black-capped Kingfisher have higher association with intake of mudskipper, crab, and small prey from mud banks.

DISCUSSION

This study reports variation in foraging behaviour among the four kingfisher species in terms of microhabitat variables and prey characteristics, and this variation can be related to the body size of each species. The mean perch height and foraging distance covered by the species showed positive

Fig. 4: Plot of the first axis of correspondence analysis (CA) ordination (91.9% of the variation) based on prey characteristics in Bhitarkanika mangroves (Jan–May, 2011)

correlation with body size. The size of the foraging niche of each species also corresponds to body size. The two smaller species, Small Blue and Collared Kingfisher, occupy comparatively smaller foraging niches than the larger species, Black-capped and Brown-winged Kingfisher. Being the smallest species, Small Blue Kingfisher is able to catch small prey and perches in lower strata of vegetation than larger kingfishers. On the contrary, the larger species, Black-capped and Brown-winged, need to catch larger prey to support their energy requirement, and therefore perch higher to be able to cover a larger area for prey. Moreover, diving from a higher perch is advantageous to gain the momentum to be able to dive into deep and/or rapid water for the larger species (Kasahara and Katoh 2008).

Similar pattern in foraging behaviour and the body size of kingfishers has been documented in previous studies. Monadjem *et al.* (1994) found that Giant Kingfisher *Megaceryle maxima* (41–46 cm) and Pied Kingfisher *Ceryle rudis* (25 cm) favoured perch-sites 2 m high, whereas the smaller species Half-collared Kingfisher *Alcedo semitorquata* (18 cm) favoured perches <2 m in height. Another study by Bonnington *et al.* (2008) along a branch of the Kilombero river in Southern Tanzania revealed that Giant and Pied Kingfisher favoured foraging areas with higher perch-sites, and deeper and wider river stretches, and Half-collared and Malachite Kingfisher *Alcedo cristata* (14 cm) preferred lower perch-sites near shallower, narrower river stretches. Kasahara and Katoh (2008) also studied the food niche differentiation between Small Blue Kingfisher (16 cm) and Greater Pied Kingfisher *Ceryle lugubris* (41–43 cm) along the Chikuma river in central Japan and found that the smaller species, i.e., Small Blue Kingfisher foraged frequently in small channels with shallow and calm water; on the contrary Greater Pied Kingfisher hunted mostly in the main channel, where the water was deep and fast-flowing.

The foraging behaviour of the smallest species, i.e., Small Blue Kingfisher, and the largest species, i.e., Brown-winged Kingfisher, is similar. They segregate in terms of prey size, which is reflected by the respective body sizes, i.e., Small Blue, the smaller species feeding more on small and medium sized prey and the larger species, i.e., Brown-winged, feeding on larger prey. Again both Collared and Black-capped feed on crabs and insects from mud banks. Probably, being the larger species, Black-capped explores other prey types as well, e.g., fish and mudskippers. Collared Kingfisher was seen preying entirely on small prey. A good portion of the diet of Black-capped Kingfisher also consisted of small prey. So this study reports that prey size partitioning between Small Blue and Brown-winged Kingfisher leads to differentiation in prey type and microhabitat use in the same area. This segregation of prey size seems to be associated with the requirements of each kingfisher species corresponding to their body sizes. Thus, foraging-niche partitioning allows these two sympatric kingfisher species to co-exist.

Table 3: Respective scores of one dimension for each category of prey characteristic variables in correspondence analysis for the four kingfisher species in Bhitarkanika mangroves (Jan–May, 2011)

Category	Scores Dimension 1
Fish	-1.79
Mudskipper	0.87
Crab	0.61
Insect	0.30
Small prey	0.58
Medium prey	-0.16
Large prey	-0.43
Water	-2.07
Mud bank	1.64
Tree hole	0.06
Vegetation	0.26
Air	0.01

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